EFFECTS OF GENOTYPE BY ENVIRONMENT INTERACTIONS ON BEEF CATTLE PERFORMANCE AT TWO LOCATIONS

BY

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to
    my parents Kepler and Verônica

to my parents-in-law
          Cid and Myrthes

to my wife, daughters and son
          Valéria, Rayanne,
          Raysla and Igor

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A total of 2592 calves produced in Nebraska and Florida were used to evaluate the importance of genotype by location interactions on the reproductive and maternal performance of eight breed groups of dam. Breed groups of dam included Angus-Hereford reciprocal crossbreds, Pinzgauer-Angus, Pinzgauer-Hereford, Brahman-Angus, Brahman-Hereford, Sahiwal-Angus and Sahiwal-Hereford.

Birth and weaning weights and preweaning average daily gain were highly influenced by the genotype-location interaction. The significant breed group of dam by location interaction observed for birth weight was the result of a reversal in rank of Brahman-Hereford and Brahman-Angus cows at the two locations. Calves from Brahman-Hereford dams in Florida were heavier at birth than those from Brahman-Angus, whereas in Nebraska, the reverse was true. The

taurus-taurus F_1 cows (Angus-Hereford reciprocal crosses and Pinzgauer crosses) weaned heavier calves at the Nebraska location than they did at the Florida location, whereas the weight of calves weaned by the zebu-taurus F_1 cows (Brahman-taurus and Sahiwal-taurus crosses) was not influenced by location. There was a change in the rank of Pinzgauer-taurus and Sahiwal-taurus dams at the two locations for preweaning calf average daily gain. Calves by Pinzgauer-taurus dams gained more weight from birth to weaning than did those from the Sahiwal-taurus dams when the comparison was made at the Nebraska location. Calves by the Sahiwal-taurus dams were superior at the Florida location.

Interactions of age of dam and breed group of dam were important sources of variation for calving difficulty score, weaning weight and preweaning gain. Regression of these three traits on age of dam revealed that the incidence of difficult parturitions decreased with age of dam, while calf weaning weight and preweaning gain increased as the dams got older. Zebu-taurus F_1 cows were much less affected by age of dam than taurus-taurus F_1 cows for all three traits.

INTRODUCTION

Researchers have long questioned whether genes superior in one environment are also superior in another environment. Many experimental results and observational reports have indicated that genetic-environmental interactions are potentially important in situations where a shift is observed in the relative performance of different genotypes under different environments.

The presence of such an interaction is likely to exist among beef cattle due to the use of proven bulls or, more generally, to the use of breeds or crosses under a wide range of environments. The range of environments is characterized not only by variations in climatic and geographical differences, but also by large differences in nutritional and management levels.

The importance of genotype-environmental interactions on beef cattle production was evaluated in this study by 1) comparing the reproductive and maternal performance of F_1 cows representing different breed groups at two different locations, 2) characterizing the performance of the different breed groups at the two locations, and 3) evaluating the importance of breed group of dam by location interactions. The two locations differ in climate, feed resource base and general management.

REVIEW OF LITERATURE

Interactions between genes within locus and between loci are examples of simple interactions involving genes. Such interactions account for the sometimes observed lack of a straightforward relationship between genes and their phenotypic effects. This lack of linearity between phenotypic response and genotype was the basis for the Lewis theory (Lewis, 1954). According to his theory, a greater stability of heterozygotes in two different environments is obtained when one allele is dominant in one environment and when the effect of that allele opposes that of the environment. He found support for this theory in an experiment conducted with tomatoes at two different temperatures, where the dominance effect of genes controlling low flower number was almost complete in the favorable environmental temperature and absent in the unfavorable temperature. Hence, greater phenotypic stability was verified for F_1's with respect to the two environments. He also provided several examples from the literature which fit his theory.

The appearance of an organism is not always that expected based on its genetic constitution. In other words, the environmental factors interact with the individual's gene pool, altering the penetrance and expressivity of individual genes. Classical examples are the Himalayan rabbit and

Siamese cat (Srb and Owen, 1952; Gardner, 1968). The Himalayan gene in a cold temperature causes darkening of the fur at the extremities. This situation can be reversed if the dark fur is removed and the animal placed in a warmer temperature. Also, the mutant tretaptera in Drosophila, which causes the balancing organs to develop into wings, has a penetrance of 35% at 25 C and 1% when the flies are raised at 17 C (Strickberger, 1976). Although these traits are controlled by one pair of genes, similar interactions should be expected for traits controlled by more than one gene pair. In fact, results obtained with domestic animals, plants and laboratory animals have shown evidence of the importance of genotype by environment interactions in swine (Fowler and Ensminger, 1957; Kristjansson, 1957; Omtvedt et al., 1962), in poultry (Dickerson, 1962), in sheep (Aboul-Naga, 1976), and in mice (Bakker et al., 1976).

Animal improvement must be based on the use of existent genetic resources. One way to utilize existing genetic variability to improve production is to capitalize on heterosis (hybrid vigor). The magnitude of heterosis will be affected by the environment in which it is estimated.

Barlow (1981) reviewed the evidence for a heterosis by environmental interaction and concluded that this interaction was the rule rather than the exception. In general, the poorer the environment, the greater the level of heterosis observed.

Homozygous individuals should be affected more by environmental variation than would be those individuals that are more heterozygous (Lerner, 1954). He defined homeostasis as "the property of the organism to adjust itself to variable conditions, or to the self-regulatory mechanisms of the organism which permit it to stabilize itself in fluctuating inner and outer environments." If heterozygous organisms are better "buffered" in a wide range of environments than are those more homozygous, and heterosis is, by definition, the deviation of the crossbred progeny mean from the parental mean, then the findings of Barlow (1981) should cause no surprise.

Two models which could be involved in a heterosis by environment interaction were reviewed by Barlow (1981). One model is based on a non-additive genetic effect by environment interaction and the other based on additive genetic effect by environment interaction. The first would fit situations in which the direction of the heterotic effect is opposite to that of the environment. Lewis (1954) showed that this situation would provide more stability for the heterozygous progenies. Barlow (1981) pointed out that this model would fit for heterosis expressed as a result of recovery from inbreeding depression, when the parental genotypes differ in a non-additive way. This model would be adequate for analyzing heterosis resulting from crosses between different breeds or divergent strains, where the parental genotypes differ in an additive fashion. In this case, recalling the definitions of homeostasis and heterosis, it can be concluded that a genotype by environment interaction should be involved.

Scientists long have been concerned with genotype by environment interactions. Darwin (1859), in his book The Origin of Species by Means of Natural Selection, mentioned that even the ancient encyclopedia of China advised caution in transporting animals from one district to another. More recently, Wright (1939) stated the possibility of the existence of nonlinearity of response between genotype and environment. In such a case, individuals should be selected within the environment in which they are to be utilized. Near the middle of the twentieth century, studies were initiated to gain more knowledge about genotype by environment interactions (Haldane, 1946; Hammond, 1947; Falconer, 1952), and a body of evidence supporting such interactions has been reported from various experiments (Burns et al., 1979; Ribeiro, 1976; Koger et al., 1979; Barlow and O'Neill, 1980; Pahnish et al., 1983). Other researchers have conducted studies over a wide range of environments and genotypes. The genotypes have varied between the extremes of identical twins to different breeds and even species. The environments studied have varied from differences in nutritional level to large climatic, management and/or geographic differences. With genotypes and environments varying in such a continuous scale, it becomes clear that the whole meaning of genotype by environment interaction is based on the magnitude of the interaction component and how to measure it becomes fundamental. There are two common procedures used to measure interactions: (1) analyzing the data in a conventional analysis of variance in a cross classified model, and (2) calculating the genetic correlation of breeding values in different environments. This second method was first introduced by Falconer (1952). He extended the idea of genetic correlation between the performance of the same genetic group in two different environments to indicate genotype by environment interaction. Robertson (1959) worked out the theoretical basis of such a measurement and extended the concept to the case where larger numbers of environments are involved. He, under the assumption that a character in different environments had the same intraclass correlation, showed that the genotype by environment interaction could be estimated by

$$r_G = \frac{A - B}{A + B - 2C} ,$$

where A, B and C are the between groups, group x environment and remainder mean squares, respectively, obtained in a two-way ANOVA table. He also showed that the interaction component of variance was related to the correlation between average breeding values in different environments. This is given by the formula

$$\sigma_{GE} = \frac{(\sigma_{G1} - \sigma_{G2})^2}{2} + 2\ \sigma_{G1}\sigma_{G2}(1-r_{G1G2}),$$

where σ_{G1} and σ_{G2} are the square roots of the genetic variance components for the character under consideration in environments 1 and 2, respectively, and r_{G1G2} is the genetic correlation of the character in each pair of environments. He also pointed out that the genetic correlation, as additional information to the analysis of variance, allows for a biological interpretation of the interaction. According to him, the genetic correlation should be .8 or less to be of biological importance. Later, Dickerson (1962) also approached the problem of more than two environments by using the concept of intraclass correlation according to the following formula:

$$r_a = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2},$$

where σ_G^2 and σ_{GE}^2 are the variance components for genotype and genotype x environment, respectively. The second point concerning to the continuity of the genotype and environmental scales is that the establishment of all possible interaction categories would become a difficult task. However, some scientists arbitrarily create different classes of combinations among "environments" and "genotypes." Dunlop (1962) proposed four different classes. He classified genotype and environment into two major classes of large and small, according to the magnitude of differences in genotype and environment. Small genetic differences would be represented by differences among individuals in a given population, while large genetic differences would be observed among different lines, strains, breeds or species. Similarly, small environmental differences would be defined as those observed among different individuals performing in the same general environment and large environmental differences would be defined as those existent among herds or regions. The combination of these two environments and genotypes would provide four different types of genotype by environment interactions. The types are

type 1-- small genetic x small environmental differences,

type 2-- small genetic x large environmental differences,

type 3-- large genetic x small environmental differences, and

type 4-- large genetic x large environmental differences.

McBride (1958) also classified the interaction between genotype and environment into four categories, which are basically the same as those proposed by Dunlop (1962). Others also had classified these interactions in different ways. Haldane (1946) proposed six types, which Mather and Jones (1958) later considered in terms of the parameters da, e_1, g_1, representing genetic, environmental, and interaction effects. The genetic quantity "da" and the environmental

"e_1" are defined as deviations, in absolute values, from the overall mean. The interaction term is defined as the amount which should be added or subtracted from each genotype-environment combination in such a way that "da" and "e_1" are orthogonal to one another and the interaction is also orthogonal to the other two. The four phenotypes expressed in terms of these three parameters are shown in table 1. Based on these, Mather and Jones (1958) specified the six qualitative relations presented by Haldane (1946) in terms of relative magnitude of da, e_1 and g_1, as can be seen in table 2. They also extended considerations to allow the inclusion of the heterozygote Aa and more than two environments.

The common denominator in all classifications discussed is the magnitude of the interactions, which in all cases can be ranked according to the ease of detection. Dunlop's type 1 classification, for instance, would be very difficult to detect, as well as types 1a and 1b of Haldane's. These types, if existent, would affect the selection procedure that should be adopted for a given population and the progress made under such a procedure, since they would influence the heritability estimates. There is, however, in addition to type 1, a transitional situation represented by type 2, which would be of extreme importance if it were a significant contributor to the total variation. It is represented by the case where individuals are selected under special environmental conditions and their performances

TABLE 1. TWO GENOTYPES AND RESULTING PHENOTYPES IN TWO ENVIRONMENTS, EXPRESSED IN TERMS OF GENETIC (da), ENVIRONMENTAL (e_1) AND INTERACTION (g_1) EFFECTS

Environment	Genotype		
	AA	aa	Mean
x	$da + e_1 + g_1$	$-da + e_1 - g_1$	e_1
y	$da - e_1 - g_1$	$-da - e_1 + g_1$	$-e_1$
Mean	da	-da	0

Mather and Jones (1958)

TABLE 2. HALDANE'S RELATIONS OF TWO GENOTYPES AND RESULTING PHENOTYPES IN TWO ENVIRONMENTS, DEFINED IN TERMS OF THE RELATIVE MAGNITUDES OF GENETIC (da), ENVIRONMENTAL (e_1) AND INTERACTIONS (g_1) EFFECTS

Haldane's Relations	Environment	Genotype AA	Genotype aa	Mather & Jones Definition
1a	x	1	3	
	y	2	4	$da>e_1>g_1$
1b	x	1	2	
	y	3	4	$e_1>da>g_1$
2	x	1	2	
	y	4	3	$e_1>g_1>da$
3	x	1	4	
	y	2	3	$da>g_1>e_1$
4a	x	1	4	
	y	3	2	$g_1>da>e_1$
4b	x	1	3	
	y	4	2	$g_1>e_1>da$

Adapted from Mather and Jones (1958)

evaluated under different environmental conditions, more practically, over a wide range of environments, as is the case in the practice of artificial insemination.

Hammond (1947) surveyed the literature and theorized that selection would be more profitable if carried out under conditions which favor complete expression of the trait. He also theorized that progress once developed could be utilized in environments different from the original, provided that other characters especially required by that new environment also were present in the animal. Falconer and Latyszewski (1952) gave a genetic interpretation for Hammond's theory, stating that it postulated that only in a good environment could genotypes be accurately estimated from the phenotypes. In other words, good environments would provide higher estimates of heritability than the poor ones. Results presented by Falconer and Latyszewski (1952), however, contradicted this theory. They found a higher heritability estimate in the poor environment, as the result of a greater decrease in environmental variance than in genetic variance. The improvement in growth obtained by selection in a good environment did not result in an improvement in growth in the poor environment. In the good environment, however, the growth of mice selected in the poor environment was almost equal to that of mice selected in the good environment. Similar evidence of genotype by environment interactions was observed by Patterson et al.

(1955), Mason and Robertson (1956), Fowler and Ensminger (1957), Robertson et al. (1960), and Van Vleck (1963).

Differences in genetic variability in different environments would lead to nonrealistic estimates of variance components. From a study of the performance of a Danish breed of dairy cattle in Denmark and two east European countries, Peterson (1975) concluded that the heritability estimates for milk production, fat content and butterfat yield were overestimated due to important genotype by environment interactions. Van Vleck (1966) verified that the sire component of variance increased with the mean, resulting in a higher heritability estimate. Similar results have been observed as a consequence of improved environment (Lytton and Legates, 1966). They verified that the intraregional analyses of milk production data resulted in larger components of variance for the northern records than for those from the southern region. Also, when the data were stratified according to production levels, the components of variance were found to be related directly to production levels. Van Vleck (1966) suggested that a transformation should be tried to verify if scale effects were causing the differences in heritability estimates.

If attention is directed now to the other end of the scale (i.e., large x large according to Dunlop [1962] or the 4a and 4b types of Haldane [1946]), it is obvious that these interactions and their effects would be much more observable and easier to detect. The complex nature of interactions causes considerable variation in results. Some clearly indicate the importance of genetic by environment interactions, resulting in genetic correlations as low as -.11 and an interaction component of variance accounting for 50-60% of the total variation. On the other hand, some results showed genetic correlation coefficients as high as 1.00, with most of them being greater than .8. In these reports, the interaction component of variance contributed 0 or near 0% of the total variation. Various reasons account for such discrepancies among results.

Certain traits can be influenced more by the interaction than others. Traits directly related to fitness should demonstrate the lowest ability to adjust to changes in environment. The magnitude of the differences between environments and between genotypes has been pointed out as one of the important factors affecting the interaction effect. But in almost all cases the variability of results seems to be related to a lack of a well defined environments and, up to certain point, to homogeneity of genotypes tested. Warwick et al. (1964) approached the problem by using 25 pairs of monozygotic twin heifers. Of the 25 pairs, 19 were purebred or grade Angus, four were Hereford, and two were Shorthorn. The twin pairs were fed equally for about a month following their arrival at the station. After that, one twin of each pair was allocated to a high concentrate ration and the other to a low concentrate ration. Average daily gain was highly affected by the ration by pair interaction. The genetic correlation between the member of a pair fed the low concentrate ration and that fed the high concentrate ration was -.11, indicating a real interaction. This interaction effect was also an important source of variation for other traits analyzed and accounted for 19% of the total variance in the case of carcass grade and 32.7% for ether extract. Kress et al. (1971b) found that none of the set by diet interactions was significant for identical twins and only one was significant for fraternal twins, when the traits analyzed were body measurement changes performed on 29 sets of twins, 15 sets of identical and 14 sets of fraternal twins. The proportion of total variance accounted for by the interaction was, on the average, close to zero, ranging from -5 to 4%. The genetic correlation between twins on different diets was lower and the environmental variation was larger for the fraternal twins than for identical twins. On the other hand, when they considered the interaction between diet and the period in which the measurement was made (nine measurements, one each 56 days) the interaction was significant for half of the traits studied. This could indicate a kind of genotype by nutrition interaction, if the period is considered as a growth curve which will be, at least partially, under genetic control. These same animals were evaluated for additional information by Kress et al. (1971a). Feed and total digestible nutrient (TDN) efficiencies were both affected by the interaction between twin set and diet. This interaction accounted for an average of 31% of the total variation. Set by diet interaction was an important source of variation for fat thickness at weaning. This reinforces what was pointed out earlier when discussing the diet by period interaction, since early fat deposition is related to early maturity. The authors also found that the twin set by diet interaction, although not significant, accounted for 23% of the total variance for the reproductive traits studied.

Feed efficiency, TDN intake and average daily gain were reported by Grass et al. (1982) to be affected by breed x diet x season of birth interactions. They used 126 animals in two experiments. The first experiment was a 2x2 factorial involving 31 pairs of twins from two breeds, Holstein and Hereford, and two diets. The second experiment involved 62 heifers out of Holstein dams and sired by four breeds of sire (Hereford, Angus, Chianina and Simmental). The results of the experiment involving twins showed that feed efficiency, TDN intake and average daily gain were affected by the breed x diet x season of birth interaction, and that the breed by diet interaction was important for the weight:height and feed:gain ratios. However, no pubertal trait studied (age, weight and height at puberty) was affected significantly by the interactions. In the second experiment, genotype by environment interactions were observed for height at 224 days of age and average daily gain in calves sired by Simmental and Chianina bulls. For traits measured at puberty, only age was not affected by this interaction. Further analyses were conducted by Hansen et al. (1982) to study the postpartum reproductive traits for three consecutive postpartum periods (PP_1, PP_2, PP_3). The differences in interval to first estrus in PP_1 and PP_2, between low and high diets, were greater for Holsteins than for Herefords. The same was true for interval to conception in PP_1, and no indication was found for breed by diet interaction in PP_3. Traits measured from days 0 to 56 postpartum were change in body weight, TDN intake and fat-corrected milk production. Only fat-corrected milk production was influenced by the breed x diet interaction in all three periods. Results from animals in experiment two showed that breed by diet interactions were an important source of variation for TDN intake in PP_1 and for fat-corrected milk and interval to first estrus in PP_2. There was also a breed of sire by diet interaction for length of gestation in PP_1 for Hereford and Simmental sired calves, which had longer gestation periods when their mothers were fed low energy diets. The opposite was true for Chianina and Angus-sired calves.

An indication of the importance of genetic adaptation to the environment was given by Kaushik et al. (1982), who utilized two different strains of Holstein-Friesians. One strain was represented by frozen semen imported from the United States and the other was represented by bulls imported from Australia or their sons. These bulls were mated with Hariana or Holstein cows and age at first calving, lactational milk yield, service period and calving interval were estimated. Purebreds as well as crossbred heifers sired by American bulls were older at first calving. No difference was found for service period or calving interval. Even though the American bulls had a higher genetic merit for milk production than those of Australian origin, the differences between purebred progeny favored the bulls with Australian background. In a similar environment, Kraüsslich (1975), cited by Syrstard (1976), compared daughters of German Friesian and American Holstein bulls in herds grouped by levels of production. The absence of an interaction between bull origin and level of herd production was verified by the fact that progeny of American bulls ranked better in all herds at all levels of production. Lawson et al. (1980) evaluated the performance of crossbred heifers, first crosses among three exotic and three British breeds, at two experimental stations in Canada. They concluded that the only trait affected by the breed cross x location interaction was 24-month weight. However, the cows were evaluated only until first calving and the authors indicated that conditions at one of the stations (Manyberries) were more rigorous for cows with calves. Rigorous conditions could favor smaller animals in subsequent calvings leading to a possible change in rank. In fact, an evaluation of the results presented by Fredeen et al. (1981), which consisted of analysis of the lifetime reproductive efficiency of these crosses, revealed this possibility. Considering Hereford-Angus cows as controls, the relative performance of Charolais-sired cows was 12.1% higher than the controls at Brandon (good environment) and 22.2% higher at Manyberries (poor environment). For the cows sired by Limousin bulls, these values were 2.2% at Brandon and -3.0% at the Manyberries location.

Rollins et al. (1964) set up an experiment to permit a study of genotype by environment interaction effects on rate of gain. Their study involved purebred Hereford and Hereford-Brahman crossbred calves evaluated in two seasons of the year. Crossbred animals outgained the purebreds both on pasture and in feedlot during the summer. However, the crossbred calves were outperformed by the Herefords in feedlot during the fall-winter season.

Nunn et al. (1978), in an attempt to evaluate the importance of region of the United States by sire interactions for birth and weaning weights, divided the country into nine regions. Records used were from the Simmental Breed Association. The results of their study led them to conclude that the sire by region interaction was unimportant in all analyses of birth weight, except for the regions of Texas-Oklahoma vs Montana. The region by sire interaction component of variance accounted for practically none of the variation, and the genetic correlation calculated, as proposed by Yamada (1962) using a mixed model, was .86 or greater for all birth weight analyses. However, the interaction seemed to be more important for weaning weight, as can be seen by the genetic correlations which ranged from .73 to .78. A similar study was done by Buchanan and Nielsen (1979), who divided the United States into five different regions according to data obtained from the American Simmental and the American Maine-Anjou Associations. Sire by region was an important source of variation for both birth and weaning weights. Sire by season interaction effects were evaluated only for the Maine-Anjou data and were an important source of variance. There also was evidence for an important sire x herd within region interaction for weaning weight but not for birth weight. The genetic correlation estimates ranged from -.12 to .77, considering sire by region interactions; from -.30 to 1.22, considering sire by season interactions; and .71, considering the interaction between sire and season. However, the estimates of genetic correlation may have been biased upwards, since they used the formula proposed by Dickerson (1962), which was developed for random models. In this case, the model was mixed and the formula proposed by Yamada (1962) would have been more appropriate.

Information from different herds raised in the northern region of the United States and in Canada was combined by Wilson et al. (1972). They concluded that herd by sire interactions within year did not affect any liveweight or carcass trait. However, it is necessary to point out that, in analyses conducted in a non-preplanned experiment like this, other sources of variation might be interferring with the results. In this study, the authors emphasized the possibility that sire by herd interactions may have been confounded with sire by genotype of dam interactions. Another interaction which, in some cases, might be included in the sire by herd or sire by region interaction is that of sire and mating system. In agreement with these results are the findings of Brown and Gacula (1962), who analyzed data from three purebred herds. They pointed out, however, that the similarity of sires within herds, some of which were as closely related as full brothers, may have tended to reduce the importance of the interaction.

As evidenced by these results, the farther apart the genotypes or the environments or both, the easier it is to find a significant interaction. Aken et al. (1976) studied data collected on bull calves sired by Fleckvieh and Gelbvieh sires at two locations, West Germany and central Texas. The genotype by environment interactions, estimated by the breed of sire by location interactions, were significant for weaning weight, weight at one year of age and yearling weight. However, when sire within breed by location was substituted in the model for breed of sire by location, there were no significant effects.

Butts et al. (1971) evaluated two lines of Hereford cattle in Florida and in Montana. After selection and establishment of the lines, half of the herd (heifers and cows) in each line was reciprocally transferred between the two locations. Genotype by environment interactions were evaluated for production and skeletal measurement traits. The authors concluded that the magnitude of such interactions observed in the experiment would indicate a need for reviewing progeny testing of sires. A further analysis was performed by Koger et al. (1979), comparing the performance of two related lines of Herefords. One of the lines was a derivative of the line originating in Montana with selection carried out in Florida and the other line was the Montana line with continued selection in Montana. Selection was based on general performance. An important line by location interaction was supported by a reversal in the rank of the two lines at the two locations for the reproductive traits measured, pregnancy and weaning rates and calf survival. These two related lines also were evaluated for weight gain and some body measurements by Burns et al. (1979). The conclusions were in perfect agreement with those from Butts et al. (1971). The local herds were superior to the introduced ones for all traits studied.

Brown et al. (1984) conducted a similar experiment where two breeds, Polled Hereford and Charolais, were evaluated. Yearling weight and yearling hip height were affected significantly by the interaction between birth location and rearing location.

An evaluation of first-cross calves of Simmental, Friesian and Brahman and straightbred Hereford calves was conducted by Barlow and O'Neill (1978) to determine the importance of breed of sire by environment interaction. A significant genotype by year interaction for average daily gain was observed as a result of Simmental x Hereford calves having the lowest growth rate among crossbred calves in some years but not in others. In agreement with this are the results of Barlow and O'Neill (1980). Their findings showed that in the poorer years the Brahman x Hereford calves grew fastest, whereas the performance of Simmental and Friesian-sired calves was better in more favorable years.

Some researchers, in an attempt to determine the importance of genotype x environment interactions, have chosen distinctive regions within a state to represent different environments. Dillard et al. (1964) used three characteristic regions in North Carolina. At each location, progenies of three sires were split between two rations, one-half was fed in feedlot and the other half was grazed on pasture. Analyses of weights and carcass measurements indicated that sire by location interaction was highly important only for separable lean in the 9-10-11 rib cut. These data also were analyzed for average daily gain by Ahlschwede et al. (1969) and the results did not indicate any evidence of sire by location or sire by ration interaction.

Nadarajah et al. (1984), in a study conducted in Virginia, reported an experiment carried out with straightbred Hereford and crossbred heifers sired by Simmental and Charolais bulls evaluated at two dissimilar locations. Nonlinear responses of the different genotypes in the two environments were observed for weights and weight gains. In the better environment, there was no difference in preweaning growth of Charolais and Simmental sired calves. However, under the harsher conditions, Simmental crosses grew less rapidly and were lighter at weaning but weighed more at 18 months of age.

As pointed out previously, traits related to fitness would be most influenced by changes in environmental conditions. If this holds true, reproductive traits which are the most important components of fitness should be expected to be most affected by genotype by environment interactions. Baker (1982), reviewing the results from breed evaluation trials in the last decade in New Zealand, stated that breed by environment interactions were particularly evident for reproductive and maternal performances. In agreement were findings of Baker et al. (1981), where marked differences in ranking of the breeds for pregnancy and weaning rates, weaning weight and cow productivity were observed when the comparisons were made in two extreme environments. Other results supporting this are presented by Kropp et al. (1973), evaluating Hereford, Holsteins and F_1 cows in the feedlot and under range conditions, and Ruvuna et al. (1983), analyzing data from Holstein, Jersey and Brown Swiss cows in the warm and cool seasons.

It should be pointed out, however, that progeny testing, a widespread practice mainly for dairy cattle, tends to select genotypes in a good environment, since such genotypes are normally selected on basis of the performance of their progeny under conditions (herd, management and nutrition) which are above average. If this is true, evaluation of these genotypes might not indicate any genotype by environment interaction if the following two conditions hold true. First, the genotypes selected are very similar, at least for traits more sensitive to environmental changes. In this case, they will respond similarly when exposed to a different condition. Second, selection resulted in different genotypes but those chosen for evaluation were not a good sample and they still respond in a similar way to a new environmental condition. Of course, the differences among such genotypes cannot be too large and the detection of genotype by environment interactions, if existent, will be very difficult.

Analyses of records from Canada's Dairy Herd Analysis Service were used by Tong et al. (1977) for evaluating the sire by herd effects on milk yield and composition traits. Sire by herd interaction accounted for 4.1, 1.1, .3, 2.6 and 5.6% of the total variation for milk, fat and protein yields and fat and protein percentages, respectively. An analysis of the heritability estimates obtained with two models, one considering and the other not considering the sire by herd interaction, allows the conclusion that milk yield and protein percent would be most affected by the sire by herd interaction. This conclusion was based on the fact that the inclusion of the interaction term in the model accounted for an important reduction in heritability estimates for these two traits. Another set of data from Canada was analyzed by Mao and Burnside (1969). They grouped the herds into 10 contrasting environments. The only important interaction involving sire was observed in herds under different levels of grain feeding during the summer. This suggested changes in the rank of sires based on the performance of their progeny fed high levels of grain and those fed on low levels. Verde et al. (1972) used information obtained from the Dairy Herd Improvement Association from Florida. The data contained milk records of the Guernsey, Jersey, and Holstein breeds. The data were analyzed to evaluate the herd by sire effects. The results agreed with most similar studies, where the interaction components accounted for 4% or less of the total variation for milk yield and 0, 5 and 14% for fat percent for Holsteins, Jerseys and Guernseys, respectively.

Trying to avoid possible inflated sampling errors due to nonorthogonality in the data as well as to avoid the confounding between bulls and herds, Kelleher et al. (1967) selected from the Iowa Dairy Herd Improvement Association those groups in which all bull-herd-season subclasses were filled. They estimated the influence of the bull-herd-season component of variance on accuracy of sire selection and concluded that the error for disregarding this interaction would not be serious unless such a component accounted for more than 10% of the total variance.

MATERIAL AND METHODS

This study included data on 2592 crossbred calves representing eight different breed combinations of F_1 dams including Hereford-Angus (HA), Angus-Hereford (AH), Pinzgauer-Angus (PA), Pinzgauer-Hereford (PH), Sahiwal-Angus (SA), Sahiwal-Hereford (SH), Brahman-Angus (BA) and Brahman-Hereford (BH).

General information on herd management, sampling of sires and dams, and procedures for generating the foundation herds was given in a series of germ plasm evaluation progress reports published by the Roman L. Hruska U.S. Meat Animal Research Center (MARC), Clay Center, Nebraska, in cooperation with Kansas State University and the University of Nebraska.

Experimental Animals

F_1 Females

The germ plasm evaluation program carried out by MARC included three distinctive cycles. Cows used in this study were from cycle III-produced, F_1 females born during the calving seasons of 1975 and 1976 at MARC. They were progenies of Hereford and Angus dams, artificially inseminated to Hereford, Angus, Pinzgauer, Sahiwal, and Brahman bulls. Semen from 13 Hereford, 16 Angus, 17 Brahman, 6 Sahiwal and 9 Pinzgauer bulls was used. The Hereford and Angus bulls were the same bulls used in the first two cycles and the Brahman bulls were sampled from purebred herds or from commercial artificial insemination enterprises. The Sahiwal calves born in the 1975 calving season were sired by two bulls, with semen from four other bulls being available in the 1975 breeding season.

Shortly after weaning in November of each year, half of each group of half-sib heifers was transferred to the Beef Cattle Research Station at Brooksville, Florida, and tne other half remained at MARC. The heifers were maintained under routine management at each location. At MARC, the heifers from 1975 calf crop were fed, for the first 41 days postweaning, a diet composed of 60% corn silage (IRN 3-08-153), 36% rolled corn (IRN 4-02-931), and 4% soybean meal (IRN 5-04-600), plus antibiotics. The diet was changed, after day 41, to one containing 80% corn silage, 14% rolled corn and 6% protein supplement. This diet was fed for 27 days. The heifers were then fed ad libitum, for 110 days, on a diet of 50% corn silage (IRN 3-08-153), 20% sorghum silage (IRN 3-04-499) and 30% alfalfa haylage (IRN 3-03-150). They were then moved to an improved cool-season pasture in April 1976. The 1976 heifers, following weaning, were fed a diet of a 60% corn silage and alfalfa haylage and 4% protein supplement (with antibiotic) for 57 days. The heifers were then placed on a diet of equal parts of corn silage and alfalfa haylage and fed ad libitum for 127 days, after which they were moved to a cool-season pasture in April 1977.

At Brooksville, Florida, the transferred heifers were managed in one group and were fed, from November to April of each year, a diet of a 20% protein range pellet, molasses (IRN 4-04-696), and grass hay. The type of hay varied according to availability of forage but consisted basically of Bahiagrass hay (IRN 1-00-462), Pangola grass (IRN 1-09-459) and Coastal Bermuda (IRN 1-00-462). Heifers were maintained on permanent grass pastures, which consisted mainly of Pensacola Bahiagrass (Paspalum notatum, Fludge).

Sires

Females at both the Florida and Nebraska locations were pasture mated, in multi-sire herds, to Red Poll and high grade (7/8) Simmental bulls selected from the herds at MARC. The Red Poll bulls were used at each location to sire the first calf crop from the eight different breed groups of dam in order to minimize dystocia. The following calf crops were sired by grade Simmental bulls. Allocation of sires to different herds was done randomly each year.

Reproductive Management

Heifers maintained at the Nebraska location were mated to calve at 2 years of age. Due to the difference in breeding seasons between Florida and Nebraska, May 15 to July 20 for Clay Center and March 15 to May 20 for Brooksville, heifers born in Nebraska and transferred to Florida did not reach puberty in sufficient time to calve as

2-year-olds. For this reason, they were bred to calve first at 3 years of age.

There was no culling of females other than that carried out for sickness, extreme unsoundness, or for being open after two consecutive breeding seasons. The number of females eliminated was small and no relationship with breed group was observed. Hence, this was considered unimportant in analyses of the data.

Cows and Calves

The cows were maintained on improved pasture from the beginning of the breeding season, mid-March at the Florida location and mid-May in Nebraska, approximately through November. They were fed legume or grass hay during the winter. Calves were born in March and April at the Nebraska location and from late December through February in Florida. All calves were identified, weighed and male calves castrated within 24-48 hours of birth. Cows were palpated for pregnancy at weaning time. A code of 0 or 1 was used to identify each animal as nonpregnant or pregnant, respectively. The cows were observed closely for indications of dystocia and all parturitions were rated from 1 through 5 according to the degree of difficulty. For the analyses of the data, these codes were grouped into 4 scores (1, 2, 4 and 6). Cows that calved with no assistance were classified as no difficulty and were given a code of 1. Cows that were given hand assistance or minor mechanical assistance were classified as presenting little difficulty and were assigned a code of 2. Those requiring major mechanical help, with no damage or minor damage to cow and/or calf, were classified as difficult and were coded 4 and those cows which required surgical calf removal, major mechanical assistance and those with abnormal presentation were assigned a code of 6.

Calves were weaned in October at the Nebraska location and in August at Brooksville, when they were approximately 218 and 201 days of age, respectively.

Statistical Analyses

Traits of primary interest were pregnancy rate, birth weight, calving difficulty, weaning weight, survival rate, and preweaning growth rate. All traits were analyzed by least squares procedures utilizing LSML76 (Harvey, 1976). The basic mathematical model included fixed effects for year, breed group of dam, location, sex of calf and first order interactions. Age of dam was included as a covariate in all analyses except survival rate, where it was not significant in preliminary analyses and was dropped from the final model. Cows nested within breed group of dam were included in the model as a random effect and were taken into account by absorption, using the maximum likelihood absorption option available in the LSML76.

Birth weight was included as a covariate in the analysis for calving difficulty, and age of calf at weaning was included as a covariate in the analysis of weaning weight.

Homogeneity of the weaning weight in relation to age of calf at weaning and age of dam between the two locations and among the eight different breed groups of dam was evaluated by the interactions involving these continuous and these class variables. The test of homogeneity for age of calf at weaning was conducted by the difference in reduction in the sum of squares when fitting different models.

Linear functions were computed for breed group of dam comparisons. Only comparisons of interest were made and the seven functions compared are shown in table 3.

Due to mathematical limitations imposed by the restrictions used in the matrix solution [($\Sigma L_i = \Sigma B_j = \Sigma LB_{ij} = 0$) where, L_i = effect of ith location, B_j = effect of jth breed group of dam, LB_{ij} = interaction of the jth breed group of dam and the ith location], only five linear desired functions involving dam breed group by location interactions were compared. These are given in table 4.

Tests for the linear functions were very sensitive, as a consequence of the large number of error degrees of freedom. Based on this, the equations for age of dam were estimated only for those dam breed groups which resulted in linear functions with t values significant at the .005 level. The linear function comparing the zebu-taurus F_1 cows (BA, BH, SA and SH) with the taurus-taurus F_1 cows (AH, HA, PA and PH) was the only one which, in all cases, revealed a t value about three times greater than any other function evaluated. Thus two different equations were

TABLE 3. LINEAR COMPARISONS AMONG THE DIFFERENT BREED GROUPS OF DAM

Comparisons[a]	AH	HA	PA	PH	BA	BH	SA	SH
Zebu-taurus vs taurus-taurus	1	1	1	1	-1	-1	-1	-1
H-dams vs A-dams	-1	1	1	-1	1	-1	1	-1
B-taurus vs S-taurus	0	0	0	0	1	1	-1	-1
AH reciprocals vs P-taurus	1	1	-1	-1	0	0	0	0
BA vs BH	0	0	0	0	1	-1	0	0
PA vs PH	0	0	1	-1	0	0	0	0
SA vs SH	0	0	0	0	0	0	1	-1

[a] Zebu-taurus = average of BA + BH + SA + SH; taurus-taurus = average of AH + HA + PA + PH; H-dams = average of the F_1 cows from Hereford dams; A-dams = average of the F_1 cows from Angus dams; A = Angus, B = Brahman, P = Pinzgauer, H = Hereford, S = Sahiwal

TABLE 4. LINEAR COMPARISONS AMONG THE DIFFERENT BREED GROUPS OF DAM-LOCATION SUBCLASSES

Comparisons[a]	Florida								Nebraska							
	AH	HA	PA	PH	BA	BH	SA	SH	AH	HA	PA	PH	BA	BH	SA	SH
Zebu-taurus vs Zebu-taurus	0	0	0	0	1	1	1	1	0	0	0	0	-1	-1	-1	-1
B-taurus vs B-taurus	0	0	0	0	1	1	0	0	0	0	0	0	-1	-1	0	0
S-taurus vs S-taurus	0	0	0	0	0	0	1	1	0	0	0	0	0	0	-1	-1
AH reciprocals vs AH reciprocals	1	1	0	0	0	0	0	0	-1	-1	0	0	0	0	0	0
P-taurus vs P-taurus	0	0	1	1	0	0	0	0	0	0	-1	-1	0	0	0	0

[a] Comparisons are between the averages at the two locations. Zebu-taurus = average of BA + BH + SA + SH; taurus-taurus = average of AH + HA + PA + PH; A = Angus, B = Brahman, P = Pinzgauer, H = Hereford, S = Sahiwal

fitted for age of dam for those traits that were affected significantly by the interaction age of dam and dam breed group. Similarly, a different equation was fitted for each location for traits which were affected by the interaction of age of dam and location.

A mixed model procedure available in LSML76 (Harvey, 1976) was used to estimate the repeatability for birth and weaning weights and calving difficulty. Standard errors of the estimates were calculated according to the formula suggested by Swiger et al. (1964).

Pregnancy rate and calving difficulty also were analyzed by the least squares procedure (Harvey, 1976). As pointed out by Harvey (1982), estimates by least squares procedure of "treatment" effects and least squares means for discrete data are unbiased. He pointed out, however, that the tests of significance for discrete data are conducted under the assumption of normality of distribution of the experimental error, and for this reason must be viewed with caution. The same is true for the standard errors of the estimates.

Harvey (1982) suggested that for a trait with binomial distribution (e.g., pregnancy rate), where the events are classified as "1" for success and "0" for failure, if $n\mu$ and $n(1-\mu)$, where μ = probability of success and n = sample size, are greater than or equal to 5 the tests of significance from a least squares analysis will be satisfactory for practical purposes.

The sums of squares for year in the different analyses were partitioned into single degree of freedom, polynomial effects to estimate any possible trend.

RESULTS AND DISCUSSION

Analyses of variance for all traits studied are shown in tables A1 through A6. Both linear and quadratic regressions of weaning weight on age of calf at weaning were found to be highly significant. Linear effects for age of dam were positive for all traits analyzed except for survival rate. A linear relationship also was verified between calving difficulty scores and birth weight of calf. The main effects studied were important sources of variation in all analyses, with the exception of breed group of dam and year. Pregnancy rate and calf survival rate were not affected (P>.10) by breed group of dam. Year effects were significant for all traits except calf survival.

Year Effects

The variability represented by effect of years is of such complexity that, in general, the response does not follow any predicted pattern. Also, in many cases, year effects contain the influences of different sires and of a changing cow herd. This leads to a complexity of influences appearing in statistical analyses as year effects. In the present case, year effects doubtless reflected a combination of influences including true year differences, sire breed of calf and age of dam. The confounding with breed of sire was due to the practice of mating heifers to Red Poll bulls to obtain small birth weights. For the second and succeeding calves, they were bred to Simmental bulls. The further confounding with age of dam was a result of all females having been produced only during the calving seasons in 1975 and 1976.

The variability of climatic conditions from year to year at the two locations probably was responsible for significant year by location interaction effects for pregnancy rate, birth weight, weaning weight and survival rate. Even though these interactions were present, inspection of year effects led to the conclusion that year was one of the main effects which contributed ($P<.001$) to the total variation in all traits analyzed, except for calf survival rate. Year effects differed at the two locations, however, as indicated by the interactions. Table 5 shows year x location least squares estimates and standard errors for pregnancy rate. Year by location interaction was the result of there being an advantage in pregnancy rate for Florida in 1981 and 1982 but an advantage for Nebraska in 1978 and 1979.

Significant year effects were found to exist for calving difficulty score. An inspection of table 6 shows a range in estimates for years from -.30 for 1979 to .33 of a score for the year 1982. Similar estimates were noted by Brinks et al. (1973), who reported year estimates varying from -.225 to .246.

TABLE 5. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR PREGNANCY RATE BY YEAR, LOCATION, AND LOCATION BY YEAR

	Year	Location	
		Florida	Nebraska
1978	.098 ± .021	-.021 ± .011	.021 ± .011
1979	-.002 ± .011	-.079 ± .009	.079 ± .009
1980	.014 ± .011	-.009 ± .009	.009 ± .009
1981	-.176 ± .021	.083 ± .009	-.083 ± .009
1982	-.100 ± .033	.025 ± .014	-.025 ± .014
Mean[a]		.012 ± .007	-.012 ± .007

[a] Overall least squares mean = .939 ± .008

TABLE 6. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR CALVING DIFFICULTY BY YEAR

Year[a]	Least Squares Estimates ± SE
1977	.20 ± .16
1978	-.14 ± .10
1979	-.30 ± .05
1980	-.15 ± .05
1981	.06 ± .10
1982	.33 ± .16

[a] Overall least squares mean = 1.12 ± .05

A year by location interaction was observed also for birth weight. As the average birth weight increased, the differences in birth weight between locations also increased (table 7). Results showing year effects on birth weight were reported by Holland et al. (1977), who concluded that year of calving affected birth weight significantly at four out of five locations studied.

Significant year effects on weaning weight were observed (table 8). Part of this effect may have been the effect of year on birth weight, an effect that persisted until weaning. Location by year interaction affected ($P<.0001$) weaning weight. There was no change in rank of weaning weight of calves at the two locations over the years. The Nebraska weaned calves were always heavier (table 8). This interaction was the result of variations in the magnitude of difference between weaning weights of calves at the Florida and Nebraska locations. An important effect of year on weaning weight of Hereford calves was reported by Harwin et al. (1966) in a study involving information collected during 17 years. Also, in agreement with the findings of this study were those of Nelson and Beavers (1982). Results reported by Barlow and O'Neill (1978) also indicated important year to year variation in weaning weight and weight changes per day of age from birth to weaning.

Survival rate also was affected ($P<.0002$) by the location by year interaction. As can be observed in table 9, the survival rate tended to be higher for those calves born

TABLE 7. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR BIRTH WEIGHT (KG) BY YEAR, LOCATION, AND LOCATION BY YEAR

	Year	Location	
		Florida	Nebraska
1978	-.40 ± .46	1.38 ± .53	-1.38 ± .53
1979	-.61 ± .29	.04 ± .33	-.04 ± .33
1980	.77 ± .23	-.65 ± .18	.65 ± .18
1981	1.70 ± .42	-.82 ± .33	.82 ± .33
1982	2.00 ± .65	.04 ± .54	-.04 ± .54
Mean[a]		-3.93 ± .13	3.93 ± .13

[a] Overall least squares mean = 32.36 ± .18 kg

TABLE 8. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR WEANING WEIGHT (KG) BY YEAR, LOCATION, AND LOCATION BY YEAR

Year		Location	
		Florida	Nebraska
1978	-3.50 ± 2.17	-.18 ± 2.51	.18 ± 2.51
1979	-.06 ± 1.37	-2.43 ± 1.55	2.43 ± 1.55
1980	5.59 ± 1.14	2.37 ± .83	-2.37 ± .83
1981	10.19 ± 1.98	-1.41 ± 1.53	1.41 ± 1.53
1982	-7.72 ± 3.01	1.65 ± 2.53	-1.65 ± 2.53
Mean[a]		-6.20 ± .69	6.20 ± .69

[a] Overall least squares mean = 224.87 ± .94 kg

TABLE 9. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR SURVIVAL RATE BY YEAR, LOCATION, AND LOCATION BY YEAR

Year		Location	
		Florida	Nebraska
1978	.01 ± .01	.01 ± .01	-.01 ± .01
1979	.00 ± .01	-.01 ± .01	.01 ± .01
1980	-.01 ± .01	.02 ± .01	-.02 ± .01
1981	.00 ± .01	-.04 ± .01	.04 ± .01
1982	.01 ± .01	.01 ± .01	-.01 ± .01
Mean[a]		.02 ± .01	-.02 ± .01

[a] Overall least squares mean = .94 ± .01

in Florida in 1978, 1980 and 1982 while there was almost no difference between the two locations in 1979 and 1981. The effect of year on calf survival rate was not significant. The lack of a significant effect for year, however, could have been diluted by the interaction effect. Koger et al. (1967), in four experimental herds in Florida, found a significant year effect on survival rate. Important year effects on survival rate ($P<.10$) also were reported by Ellis et al. (1979).

Breed Group of Dam and Its Interaction With Other Effects

Interactions involving dam breed group were, in general, important sources of variation.

Least squares estimates and standard errors for pregnancy rate by dam breed groups are shown in table 10. There was no significant effect of breed group of dam or breed group of dam by location interaction on pregnancy rate. The sum of squares for this interaction accounted for .36% of the total mm of squares. The lack of significant breed of cow effect on pregnancy rate also was reported by Nelson and Beavers (1982), in a study involving purebred Angus, Hereford, Charolais, and Brown Swiss cows. The results verified in this study are in contrast with the findings of Koger et al. (1979), who observed a reversal in rank for pregnancy rate in two lines of Herefords studied at Montana and Florida locations.

The least squares analysis for calving difficulty did not include location effect, since the analysis for this

TABLE 10. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR PREGNANCY RATE BY BREED GROUP OF DAM

Breed group of dam[a]	L.S. Estimates ± SE
Hereford-Angus	.00 ± .01
Angus-Hereford	.01 ± .02
Pinzgauer-Angus	-.02 ± .01
Pinzgauer-Hereford	.00 ± .02
Brahman-Angus	.00 ± .01
Brahman-Hereford	.00 ± .02
Sahiwal-Angus	-.01 ± .01
Sahiwal-Hereford	.00 ± .02
Overall L.S. mean	.93 ± .01

[a] Breed of sire of dam shown first

trait was carried out only on data from Nebraska. The estimated repeatability for calving difficulty in this study was .04±.02. The effects of breed group of dam and interaction between breed group of dam and sex of calf influenced calving difficulty scores, $P<.0001$ and $P<.07$ respectively. Least squares estimates for calving difficulty by sex of calf and by breed group of dam-sex of calf subclasses are shown in table 11. Sahiwal and Brahman-sired dams (zebu-taurus) experienced less calving difficulty ($P<.005$) than dams of the other breed groups. In addition, calves out of these zebu-taurus F_1 dams were lighter at birth than those out of taurus-taurus F_1 dams. These results are in agreement with the findings of Cundiff et al. (1984).

Factors other than birth weight are involved in calving difficulty. Two traits which seem to be important are calf conformation and pelvic area of the cow. Laster (1974) pointed out that although differences in dystocia rates among breeds with similar birth weights suggested calf conformation as a possible effect, the calf measurements studied did not show any relationship with dystocia. On the other hand, part of the difference in calving difficulty score can be attributed to differences in pelvic area, as indicated by the findings of Bellows et al. (1971) who reported that pelvic area of the dam had a significant negative effect on calving difficulty score in Angus and Hereford cows. These results agree with those found by Rice and Wiltbank (1970), who concluded that 2-year old Hereford

TABLE 11. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR CALVING DIFFICULTY BY BREED GROUP OF DAM, SEX OF CALF, AND SEX OF CALF BY BREED GROUP OF DAM

Breed group of dam[a]		Sex of Calf	
		Male	Female
HA	.27 ± .06	.06 ± .05	-.06 ± .05
AH	.08 ± .09	.03 ± .07	-.03 ± .07
PA	.06 ± .07	.10 ± .05	-.10 ± .05
PH	.13 ± .08	.07 ± .06	-.07 ± .06
BA	-.14 ± .07	-.10 ± .05	.10 ± .05
BH	-.15 ± .08	-.07 ± .06	.07 ± .06
SA	-.13 ± .08	-.02 ± .05	.02 ± .05
SH	-.11 ± .09	-.07 ± .06	.07 ± .06
Mean[b]		.06 ± .02	-.06 ± .02

[a] A = Angus, H = Hereford, P = Pinzgauer, B = Brahman, S = Sahiwal, with breed of sire of dam shown first

[b] Overall least squares mean = 1.12 ± .05

heifers with pelvic areas less than 200 cm^2 showed dystocia rates more than twice as high as those with pelvic areas larger than 200 cm^2.

The lower incidence of calving difficulty found in this study among the zebu-taurus cross cows might suggest the possibility of a heterotic effect on pelvic area. The amount of heterosis expected from the zebu-taurus cross should be much greater than that expected from taurus-taurus cross (Koger, 1980). On the other hand, practical experience has shown repeatedly that calving difficulty is less frequent in zebu and zebu cross cows than in cows of European breeding. This might indicate that the low calving difficulty scores observed in zebu-taurus crosses in this study were the result of an additive genetic effect rather than a consequence of heterosis. Laster et al. (1973) reported no effect of heterosis on dystocia scores for Angus-Hereford reciprocal crossbred cows.

The significant breed group of dam by sex interaction effect on calving difficulty was due to the magnitude of the difference between bull and heifer calves from the different breed groups of dam. This difference was greater among taurus-taurus F_1 cows than among zebu-taurus F_1 cows. Table 11 shows the least squares estimates for this interaction. Female progeny of Brahman-Angus cows tended to result in higher calving difficulty scores than the male progeny. The opposite was observed for Sahiwal-Angus F_1 cows, and no difference was observed for parturitions involving males or females calves out of Brahman or Sahiwal-Hereford F_1 cows. Among the taurus-taurus F_1 cows, however, there was a higher percentage of calving difficulty in parturitions involving male calves than in those involving female calves. Breed of dam by sex of calf interaction also was found to have a significant effect on calving difficulty in a study involving Angus, Hereford and their reciprocal crosses (Sagebiel et al., 1969). Crossbred dams giving birth to female calves had significantly higher calving difficulty scores than their purebred counterparts. Conversely, Bellows et al. (1971) reported that average calving score for male calves exceeded ($P<.01$) that for females by .74 and .40 for Angus-Hereford and Hereford-Angus cows, respectively.

Interactions involving breed group of dam were an important source of variation for birth weight. A genotype (breed group of dam) by sex of calf interaction also was present in this study. The least squares estimates for the breed group of dam-sex of calf classes are given in table 12. Calves out of taurus-taurus F_1 females showed greater differences in birth weight between sexes than those out of zebu-taurus F_1 cows ($P<.005$). Apparently the greater dimorphism between sexes exhibited by European breeds might be responsible, at least, in part, for this interaction. Seifert and Kennedy (1966) and Barlow and O'Neill (1978) reported greater differences between sexes among Bos indicus-British crossbred calves than among British-British

TABLE 12. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR BIRTH WEIGHT (KG) BY BREED GROUP OF DAM, SEX OF CALF, AND SEX OF CALF BY BREED GROUP OF DAM

Breed group of dam[a]		Sex of Calf	
		Male	Female
HA	-.06 ± .31	.31 ± .20	-.31 ± .20
AH	-.04 ± .37	.48 ± .28	-.48 ± .28
PA	3.14 ± .31	.53 ± .21	-.53 ± .21
PH	3.81 ± .37	.12 ± .25	-.12 ± .25
BA	-.19 ± .30	.08 ± .21	-.08 ± .21
BH	.00 ± .34	-.25 ± .25	.25 ± .25
SA	-3.85 ± .32	-.80 ± .23	.80 ± .23
SH	-2.82 ± .35	-.47 ± .26	.47 ± .26
Mean[b]		.94 ± .28	-.94 ± .28

[a] A = Angus, H = Hereford, P = Pinzgauer, B = Brahman, S = Sahiwal, with breed of sire of dam shown first

[b] Overall least squares mean = 32.36 ± .18 kg

crossbred calves. A similar interaction was reported by Barlow and O'Neill (1980). They studied four different crosses, and the Simmental-Hereford ranked highest according to birth weight of the female calves, while Brahman-Hereford ranked highest based on birth weight of the male calves.

A more careful inspection of these results indicated an association between birth weight of calf and magnitude of the difference in birth weight between sexes. A rank correlation test performed on the results revealed a correlation of .48 between average birth weight and difference in birth weights of female and male calves, which supported the conclusion that the data do not provide enough evidence to reject the hypothesis of no rank correlation between birth weight and magnitude of the difference between the weights of female and male calves. Thus, the interaction seems to be a consequence of a scale effect; the heavier the calves at birth, the larger the differences between sexes. Submission of the data of Barlow and O'Neill (1978; 1980) to the same test showed a perfect rank correlation between genotype means and magnitude of the difference between sexes.

Breed group of dam affected ($P<.0001$) calf birth weight. The heaviest calves were out of Pinzgauer-sired cows and the lightest calves were those out of Sahiwal-sired cows. Calf birth weight also was dependent on the interaction between breed group of dam and location where the calf was born (table 13). Breed group of dam by

TABLE 13. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR BIRTH WEIGHT (KG) BY BREED GROUP OF DAM, LOCATION, AND LOCATION BY BREED GROUP OF DAM

Breed group of dam[a]		Location	
		Florida	Nebraska
HA	-.06 ± .31	-.47 ± .31	.47 ± .31
AH	-.04 ± .37	-1.12 ± .36	1.12 ± .36
PA	3.14 ± .31	-.01 ± .31	.01 ± .31
PH	3.81 ± .37	-.56 ± .36	.56 ± .36
BA	-.19 ± .30	1.05 ± .30	-1.05 ± .30
BH	.00 ± .34	.31 ± .34	-.31 ± .34
SA	-3.85 ± .32	.75 ± .32	-.75 ± .32
SH	-2.82 ± .35	.06 ± .35	-.06 ± .35
Mean[b]		-3.93 ± .13	3.93 ± .13

[a] A = Angus, H = Hereford, P = Pinzgauer, B = Brahman, S = Sahiwal, with breed of sire of dam shown first

[b] Overall least squares mean = 32.36 ± .18 kg

location interaction accounted for less than 1% of the total variability of birth weight. This interaction was the result of a reversal in rank of Brahman-Hereford and Brahman-Angus cows at the two locations. Calves out of Brahman-Hereford dams were heavier ($P<.005$) at birth than those out of Brahman-Angus in Florida, while the reverse was true in Nebraska. Heavier birth weights for calves by Hereford dams also were observed by Gregory et al. (1979), who reported that these calves were 2.4 kg heavier than those from Angus dams. Averaged over location, calves out of taurus-taurus F_1 females outweighed those of zebu-taurus F_1 females at birth. However, this primarily was due to the difference between the two extreme groups, Pinzgauer-taurus F_1 cows which produced the heaviest and Sahiwal-taurus F_1 cows which produced the lightest calves. The presence of this genotype by environment interaction for birth weight emphasizes that selection carried out in different environments might result ultimately in different genotypes. Repeatability of birth weight was estimated as a cow trait by the correlation among birth weights of calves by the same cow. The repeatability estimate for this trait was .18±.05. Likewise, the repeatability for weaning weight was .37±.26.

The linear functions evaluated (table 4) showed an interesting interaction between genetic group and location. This interaction represented 3.3% of the total sum of squares observed for weaning weight. The superiority observed in Florida for birth weights of Brahman-Hereford over those recorded for Brahman-Angus was not observed for weaning weight. A closer evaluation of the eight breed groups of dam indicated that they could be grouped into four groups according to weaning weight of their calves (Angus-Hereford and their reciprocals, Brahman-taurus, Pinzgauer-taurus and Sahiwal-taurus). The importance of the genotype by environment interaction for weaning weight was evidenced by comparing the dam breed group rankings in Florida with those in Nebraska (tables 14 and 15). It also is of interest to note the change in rank of Pinzgauer and Sahiwal crosses between the two locations. Progeny of Pinzgauer-taurus dams weaned heavier than those of Sahiwal-taurus in Nebraska. Calves by Sahiwal-taurus dams were superior in Florida.

Clearly, taurus-taurus F_1 cows (Angus-Hereford and their reciprocals along with the Pinzgauer crosses) weaned heavier calves in the Nebraska location than they did at the Florida location, while the weights of calves out of zebu-taurus group (Brahman-taurus and Sahiwal-taurus crosses) were not influenced greatly by the location at which the calves were produced. The calves from zebu-taurus were the heaviest groups at both locations; however, their advantage over the taurus-taurus groups at the Nebraska location was much smaller than at the Florida location.

These results could be consequence of a combination of hybrid vigor and a possible hybrid vigor-location

TABLE 14. COW PERFORMANCE BY BREED GROUP OF DAM AND LOCATION, MEASURED BY WEANING WEIGHT OF CALF

Cow breed group[a,b]	Location	
	Florida	Nebraska
AH + HA	78	89
PA + PH	85	96
BA + BH	100	100
SA + SH	94	94

[a] Cow performance by breed group is expressed as a percent of the weaning weight of calves by BA and BH dams

[b] A = Angus, H = Hereford, P = Pinzgauer, B = Brahman, S = Sahiwal, with breed of sire of dam shown first

TABLE 15. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR WEANING WEIGHT (KG) BY BREED GROUP OF DAM, LOCATION, AND LOCATION BY BREED GROUP OF DAM

Breed group of dam[a]		Location	
		Florida	Nebraska
HA	-24.90 ± 1.46	-7.36 ± 1.45	7.36 ± 1.45
AH	-16.55 ± 1.67	-5.95 ± 1.66	5.95 ± 1.66
PA	-5.24 ± 1.43	-6.83 ± 1.43	6.83 ± 1.43
PH	-2.56 ± 1.70	-7.18 ± 1.69	7.18 ± 1.69
BA	19.67 ± 1.39	6.68 ± 1.39	-6.68 ± 1.39
BH	19.37 ± 1.58	6.46 ± 1.58	-6.46 ± 1.58
SA	4.14 ± 1.45	7.48 ± 1.45	-7.48 ± 1.45
SH	6.06 ± 1.61	6.69 ± 1.61	-6.69 ± 1.61
Mean[b]		-6.20 ± .69	6.20 ± .69

[a] A = Angus, H = Hereford, P = Pinzgauer, B = Brahman, S = Sahiwal, with breed of sire of dam shown first

[b] Overall least squares mean = 224.87 ± .94 kg

interaction. Interactions of the same nature, where the more adapted excelled, also were reported by Butts et al. (1971). They observed that weaning weight tended to be higher for calves evaluated under the environment in which their parent line originated. Thus, calves from the herds selected in Montana were 8.2 and 17.2 kg heavier at weaning than calves from the herds selected in Florida, when the comparison was carried out in Montana. In Florida, however, the heavier calves at weaning were those from the herds selected in Florida. On the other hand, Wilson et al. (1972), looking at the importance of herd by sire within year interaction in two different breeds, Angus and Hereford, did not find interactions approaching significance for weaning weight. Other evidence of the importance of genotype by environment interactions was provided by Reynolds et al. (1982). They found that the year by breed of calf interaction was significant for several traits, including 205-day adjusted weight. Burns et al. (1979), evaluating the data from phase 2 of the study comparing two Hereford lines, concluded that the advantages for the local over the introduced groups observed in phase 1 (Butts et al., 1971) were still present. Genotype by environment interactions also were evident in the study conducted by Peacock et al. (1969). They found highly significant effects for breed by pasture and breed by year interactions on calf weaning weight. Changes in rank of breeds in different environments also were reported by Baker et al.

(1981) who, in an evaluation study involving 11 breed groups at two extreme environments in New Zealand, verified that under good environmental conditions the Simmental crosses ranked second but ranked only seventh under the harsher environment.

Estimates for weaning weight by breed group of dam-sex of calf classification are shown in table 16. The larger differences observed for birth weight between male and female progeny of the taurus crossbred dams were not present at weaning. An interaction effect of sex of calf and breed group of dam on weaning weight might be expected when the breed groups differ markedly in milk production. The greater growth potential of the male calves could be expressed more fully when they were nursing dams with greater milk production.

In the present study, zebu-taurus F_1 dams produced the heaviest calves at weaning ($P<.005$). The estimates for the zebu-taurus F_1 dams ranged from 4.14 for Sahiwal-Angus to 19.67 kg for Brahman-Angus, while those for taurus-taurus F_1 dams ranged from -24.90 for Hereford-Angus to -2.56 kg for Pinzgauer-Hereford cows (table 16).

Survival rate was not influenced ($P>.61$) by breed group of dam or by any of the interactions involving this effect. The least squares estimates for the interaction of survival rate by breed group of dam are shown in table 17. This interaction accounted for only 1% of the total variability.

TABLE 16. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR WEANING WEIGHT (KG) BY BREED GROUP OF DAM, SEX OF CALF, AND SEX OF CALF BY BREED GROUP OF DAM

Breed group of dam[a]		Sex of Calf	
		Male	Female
HA	-2.490 ± 1.46	-1.43 ± .97	1.43 ± .97
AH	-16.55 ± 1.67	-.46 ± 1.26	.46 ± 1.26
PA	-5.24 ± 1.43	-.35 ± 1.06	.35 ± 1.06
PH	-2.56 ± 1.70	-1.45 ± 1.22	1.45 ± 1.22
BA	19.67 ± 1.39	1.42 ± .99	-1.42 ± .99
BH	19.37 ± 1.58	1.35 ± 1.18	-1.35 ± 1.18
SA	4.14 ± 1.45	-.92 ± 1.05	.92 ± 1.05
SH	6.06 ± 1.61	1.83 ± 1.21	-1.83 ± 1.21
Mean[b]		7.51 ± .42	-7.51 ± .43

[a] A = Angus, H = Hereford, P = Pinzgauer, B = Brahman, S = Sahiwal, with breed of sire of dam shown first

[b] Overall least squares mean = 224.87 ± .94 kg

TABLE 17. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR SURVIVAL RATE BY BREED GROUP OF DAM

Breed group of dam[a,b]	L.S. Estimates ± SE
Hereford-Angus	-.00 ± .02
Angus-Hereford	.02 ± .02
Pinzgauer-Angus	-.01 ± .02
Pinzgauer-Hereford	-.03 ± .02
Brahman-Angus	.02 ± .02
Brahman-Hereford	-.02 ± .02
Sahiwal-Angus	.01 ± .02
Sahiwal-Hereford	.01 ± .02

[a] Breed of sire of dam shown first

[b] Overall least squares mean = .94 ± .01

Approximately 3% of the total variability in preweaning weight gain was accounted for by the breed group of dam by location interaction. Calves by the zebu-taurus dams had a higher average daily gain from birth to weaning at both locations than those by the taurus-taurus dams (table 18). However, the difference between the progeny of the zebu-taurus F_1 dams and those from taurus-taurus F_1 dams was much less in Nebraska than in Florida. These results indicated that infusion of zebu blood by crossbreeding led to a superior performance in the two contrasting environments, while the Bos taurus crossbreds performed considerably worse in the subtropical environment of Florida than they did in the temperate climate of Nebraska. However, the zebu-taurus and taurus-taurus crossbred groups can be subdivided further into four groups which are Angus-Hereford crosses, Pinzgauer-taurus, Brahman-taurus and Sahiwal-taurus. Analysis of these four groups (table 19) indicated a change in the rank of calves from Pinzgauer-taurus and Sahiwal-taurus dams at the two locations. Calves by Pinzgauer-taurus dams gained more weight from birth to weaning at the Nebraska location than did those from the Sahiwal-taurus dams, while calves by the Sahiwal-taurus dams were superior at the Florida location. Progeny of the Brahman-taurus F_1 dams were superior to the progeny of the other three breed groups of dam in Florida, and to progeny of the Angus-Hereford reciprocals and Sahiwal-taurus dams in Nebraska. The lowest average daily gains from birth to weaning, at

TABLE 18. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR AVERAGE DAILY GAIN (KG) FROM BIRTH TO WEANING BY BREED GROUP OF DAM, LOCATION, AND LOCATION BY BREED GROUP OF DAM

Breed group of dam[a]		Location	
		Florida	Nebraska
HA	-.116 ± .006	-.027 ± .006	.027 ± .006
AH	-.078 ± .007	-.019 ± .007	.019 ± .007
PA	.038 ± .006	-.030 ± .006	.030 ± .006
PH	.026 ± .007	-.027 ± .007	.027 ± .007
BA	.092 ± .006	.022 ± .006	-.022 ± .006
BH	.096 ± .007	.027 ± .007	-.027 ± .007
SA	.033 ± .006	.028 ± .006	-.028 ± .006
SH	.038 ± .007	.027 ± .006	-.027 ± .006
Mean[b]		-.018 ± .002	.018 ± .002

[a] A = Angus, H = Hereford, P = Pinzgauer, B = Brahman, S = Sahiwal, with breed of sire of dam shown first

[b] Overall mean = .908 ± .004 kg

TABLE 19. COW PERFORMANCE BY BREED GROUP OF DAM AND LOCATION, MEASURED BY CALF PREWEANING AVERAGE DAILY GAIN

Cow breed group[a,b]	Location	
	Florida	Nebraska
AH + HA	76	86
PA + PH	89	100
BA + BH	100	100
SA + SH	94	94

[a] Cow performance by breed group is expressed as percent of the average daily gain of calves by BA and BH dams

[b] A = Angus, H = Hereford, P = Pinzgauer, B = Brahman, S = Sahiwal, with breed of sire of dam shown first

both locations, were by those progeny of the Angus-Hereford reciprocals. The difference between the progeny of the Brahman-Hereford F_1 dams and those from Angus-Hereford reciprocal F_1 dams was much less in Nebraska than in Florida.

A genotype by environment interaction for average daily gain was observed by Carrol et al. (1955) who found that Brahman-Hereford crossbred steers outperformed straightbred Herefords during the summer months, while no difference was found between the two groups for gain during winter and fall. Burns et al. (1979) also reported evidence of such an interaction in a study involving two lines of Hereford cattle evaluated at two different locations (Montana and Florida). The local line had higher gains than the introduced one.

The breed group of dam by sex of calf interaction also was significant for average daily gain, and the least squares estimates shown in table 20 indicate that sex differences increased as the dam breed group average increased. The rank correlation was .86 ($P<.01$). This interaction, as pointed out earlier, may have been a result of better milk production by zebu-taurus F_1 dams, which would have permitted a fuller expression of the growth potential by the male calves. A similar interaction was found to be important by Pani et al. (1977), who reported an important sire by sex of calf interaction for average daily gain in Hereford calves.

TABLE 20. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR AVERAGE DAILY GAIN (KG) FROM BIRTH TO WEANING BY BREED GROUP OF DAM, SEX OF CALF, AND SEX OF CALF BY BREED GROUP OF DAM

Breed group of dam[a]		Sex of Calf	
		Male	Female
HA	-.116 ± .006	-.008 ± .004	.008 ± .004
AH	-.078 ± .007	-.006 ± .005	.006 ± .005
PA	.038 ± .006	-.004 ± .004	.004 ± .004
PH	.026 ± .007	-.007 ± .005	.007 ± .005
BA	.092 ± .006	.006 ± .004	-.006 ± .004
BH	.096 ± .007	.009 ± .005	-.009 ± .005
SA	.033 ± .006	-.001 ± .004	.001 ± .004
SH	.038 ± .007	.010 ± .005	-.010 ± .005
Mean[b]		.032 ± .002	-.032 ± .002

[a] A = Angus, H = Hereford, P = Pinzgauer, B = Brahman, S = Sahiwal, with breed of sire of dam shown first

[b] Overall least squares mean = .908 ± .004 kg

Sex of Calf

The interaction between sex of calf and breed group of dam was significant for all traits studied, except weaning weight and calf survival rate.

The sex ratio at birth for the 2592 calves in this study was 1311 males to 1281 heifers. As shown in table 11, the frequency of difficult births for male calves was greater ($P<.0001$) than for females. The average calving difficulty score registered for dams giving birth to male calves was .13 of a score higher than the average calving difficulty score assigned to dams producing female calves. These results agree with others indicating that sex is an important factor affecting calving difficulty and that, in general, male calves are responsible for more difficult parturitions than are female calves (Lasley et al., 1961; Brinks et al., 1973; Sagebiel et al., 1969; Bellows et al., 1971; Laster et al., 1973). This effect of sex of calf on calving difficulty indicates that there might be other factors associated with male calves which lead to more calving difficulty than could be accounted for only by their heavier birth weights and age of dam. Results obtained by Bellows et al. (1971) indicated that gestation length was not a factor responsible for the greater calving difficulty observed for male calves. The authors agreed that differences in conformation between male and female calves could have been responsible for the differences noted, but they also emphasized the possibility of this difference being a result of other factors such as hormonal differences.

Least squares estimates for birth weight by sex of calf are given in table 12. Males calves were 6.0% heavier at birth ($P<.0001$) than female calves. This difference was similar to that reported in the literature. Laster et al. (1973) found that males were 8% heavier at birth than female calves, and Lasley et al. (1961) reported a 3% difference in favor of male calves.

The superiority of steer calves was still present at weaning with male calves being 6.9% heavier ($P<.0001$) than female calves (table 16). This sex difference in weaning weight has been well documented (Koger and Knox, 1945; Koch and Clark, 1955; Euclides Filho, 1977). Sex of calf also had an effect ($P<.006$) on survival from birth to weaning, with heifer calves having a higher survival rate than the steer calves (table 21). The survival rate of the heifers was 2.2% more than of the males. The higher mortality rate among male progeny may have been related to the higher levels of calving difficulty experienced by the males (table 11). Eighty-nine percent of the calves experiencing difficult delivery were male calves.

Least squares average daily gain from birth to weaning for all calves in this study was .91 kg (table 20). Male calves gained more weight ($P<.0001$) than females with estimates being .03 and -.03 for male and female calves, respectively. These results are in agreement with those found by

TABLE 21. LEAST SQUARES ESTIMATES AND STANDARD ERRORS FOR SURVIVAL RATE BY SEX OF CALF

Sex of calf[a]	L.S. Estimates ± SE
Male	-.014 ± .005
Female	.014 ± .005

[a] Overall L.S. mean = .937 ± .007

Gregory et al. (1979), who reported that male calves gained .065 kg more per day than female calves and those of Reynolds et al. (1982) who reported a difference of .068 kg more per day in favor of male calves.

Location

Location differences in this study were associated with a combination of environmental effect differences, such as climate, nutrition, etc. Location was involved in significant interactions with either dam breed group or year for all traits studied. The least squares estimates for pregnancy rate by location are shown in table 5. The Florida location showed a superiority of approximately 3% over the Nebraska location in pregnancy rate. Pregnancy rates were 95 and 92%, respectively, at the Florida and Nebraska locations. The analysis of survival rate also revealed an advantage of approximately 4.4% for the Florida location (table 9). These two traits combined gave an advantage of 8.9% in weaning rate for the Florida location which in combination with weaning weight resulted in 3.6% more weight of calf weaned per cow exposed to breeding at the Florida location (table 22). Table 22 shows the weaning weight per cow exposed to breeding by location and by breed group of dam-location subclasses. The calf weight at weaning per cow exposed followed the same general pattern demonstrated by weaning weight. The zebu-taurus F_1 cows were superior to the taurus-taurus F_1 at both locations. However, the magnitude of the difference between calf weaning weight/cow

TABLE 22. LEAST SQUARES MEANS FOR PERFORMANCE TRAITS BY LOCATION AND BREED GROUP OF DAM

	Florida				Nebraska			
Breed group of dam	Pregnancy rate	Survival rate	Weaning weight	Weaning weight /cow	Pregnancy rate	Survival rate	Weaning weight	Weaning weight /cow
Angus-Hereford	.93	.99	196	180	.96	.93	220	196
Hereford-Angus	.98	.95	186	173	.90	.92	214	177
Pinzgauer-Angus	.92	.92	206	174	.91	.92	233	195
Pinzgauer-Hereford	.98	.93	209	190	.89	.89	236	187
Brahman-Angus	.93	.98	245	223	.94	.92	244	211
Brahman-Hereford	.94	.96	244	220	.94	.88	244	202
Sahiwal-Angus	.94	.97	230	210	.91	.92	228	191
Sahiwal-Hereford	.95	.97	231	213	.92	.93	230	197
Overall L.S. mean	.95	.96	219	200	.92	.91	231	193

Overall least squares means = .93, .93, 225 and 195, respectively, for pregnancy rate, survival rate, calf weaning weight, and kg of calf weaned per cow exposed to breeding.

exposed in these two crossbred cow groups was much less at the Nebraska location.

Regressions

Three continuous variables, age of dam, age of calf at weaning and birth weight, were used where appropriate in the analyses of the different traits studied.

Changes which result from the aging process can be responsible for the effect of age of dam on traits measured on the cow and on traits measured on her calves. Age of dam significantly affected the traits analyzed, with the exception of survival rate.

Differences in nutritional environment, in particular, and in management, in general, can lead to an interaction between the age of dam effect and "environment." Differences in genotype can also lead to an interaction between age of cow and genotype of cow. In this study, however, the age of dam effect is a combination of age of dam, breed of sire, and possibly some effect of years, since all females were mated with Red Poll bulls to produce their first calf and with Simmental bulls for all subsequent calves. Also, all females were born in a 2-year period; thus, age of dam is confounded partially with years.

The interaction of age of dam and breed group of dam was an important source of variation ($P<.0001$) for calving difficulty score, weaning weight, and average daily gain from birth to weaning.

Age of dam had a linear effect on pregnancy rate, with the percentage of pregnant cows increasing according to the equation

$$\text{Pregnancy Rate} = .93+.05\ (\text{Dam Age} -4.18).$$

Regression of calving difficulty on age of dam showed that the number of difficult parturitions decreased with age of dam and that the zebu-taurus F_1 cows were much less affected by age of dam than were taurus-taurus F_1 cows. This is shown by the regression equations

$$\text{Calving Difficulty} = .98-.13\ (\text{Dam Age} -4.18)$$

and

$$\text{Calving Difficulty} = 1.25-.38\ (\text{Dam Age} -4.18)$$

for zebu-taurus and taurus-taurus groups, respectively. A similar interaction was found by Brinks et al. (1973), who reported a significant interaction between age of dam and inbreeding level of dam for parturition score. Also, Laster et al. (1973) concluded that the difference in percent calving difficulty was greater between Hereford and Angus 2-year-old cows than between Hereford and Angus cows that were 3, 4, and 5 years of age.

In beef cattle, age of dam is known to affect both birth and weaning weights of calves. The effect of age of dam on birth weight might be related to the incomplete development of reproductive organs as well as the skeleton in young females, which results in smaller calves at birth. The effect on weaning weight has been shown to be related to the increases in milk production with increasing age, up to 5 or 6 years of age. Thus, age of cow can be considered as an important "environment" for the calf and, thus, any interaction between age of dam and dam breed group would indicate a genotype by environment interaction of some type.

Assuming age of dam to be a measure of "environment" implies that an interaction between age of dam and location would represent an interaction between specific and general environments. However, the relationships of age of dam with the birth and weaning weights of the calf and with milk production of the dam indicate that weaning weight of the calves can be used indirectly as a measure of rate of maturity of the dam. Rate of maturity is a genetically controlled trait, and it is largely determined by different animal attributes such as size, species, type (beef or milk), level of milk production and, obviously, breed. Thus, in a comparison involving different breeds of dam, an important interaction between location and age of dam that affects weaning weight of the calf would represent a genotype by environment interaction which might be a result of different breeds maturing at different rates at the different locations. Different rates of maturity of the dams would be responsible, in turn, for the ultimate effect on calf weaning weight, since milk production tends to increase as the cow matures, plateaus, and then decreases with advancing age.

In this study, the interaction between age of dam and location was significant only for birth weight. Age of dam had much more effect on birth weight of calves born in Florida than on birth weight of calves born in Nebraska. The regression equations for birth weights were

Birth Weight = 28.43+1.39 (Dam Age -4.18)

and Birth Weight = 36.29+.15 (Dam Age -4.18),

respectively, for calves born at Florida and Nebraska locations.

There was a significant (P<.0001) interaction between age of dam and breed group of dam for weaning weight. The weaning weight of calves from zebu-taurus F_1 cows were less affected by age of dam than were calves out of taurus-taurus F_1 cows. The regression equations were

Weaning Weight = 237.18+8.21 (Dam Age -4.18)

and Weaning Weight = 212.56+.15 (Dam Age -4.18)

for zebu-taurus and taurus-taurus F_1 breed of dam groups, respectively. A similar pattern was observed for average daily gain, with the regression equations being

Average Daily Gain = .97+.03 (Dam Age -4.18)

and Average Daily Gain = .84+.09 (Dam Age -4.18),

respectively, for calves by zebu-taurus and taurus-taurus F_1 dams.

Age of calf at weaning had a quadratic effect on calf weaning weight. According to Wilson et al. (1972), the adjustment for weaning age should be done in analyses even though weaning and yearling weights may have been adjusted previously to a constant age. However, it should be pointed out that this procedure can lead to over adjustment of the weaning weight for calves born early in the calving season.

No interaction was observed between age of calf at weaning and location or between age of calf and breed group of dam. Thus, a pooled quadratic equation for age of calf at weaning was fitted. This equation was

$$\text{Age of Calf at Weaning} = 224.87 + .72\ (\text{Calf Age} - 206.86) - .004\ (\text{Calf Age} - 206.86)^2.$$

According to this equation, calves born earlier in the calving season were lighter at weaning than those born later. These results are in agreement with the findings of Lasley et al. (1961), Wilson et al. (1972), and Holland et al. (1977).

Birth weight affected ($P<.0001$) calving difficulty. Various authors (Bellows et al., 1971; Laster et al., 1973; Laster, 1974) have suggested that size of calf at birth is one of the most important factors affecting calving difficulty.

As indicated by the equation

$$\text{Calving Difficulty} = 1.12 + .009\ (\text{Birth Weight} - 36.33),$$

calving difficulty increased as birth weight increased. This finding is in agreement with that of Laster et al. (1973), who reported a 1% increase in assisted parturitions as the result of a 1 kg of increase in birth weight of the calf. Bellows et al. (1971) analyzing data from Angus and Hereford cattle, reported regression coefficients for calving difficulty on birth weight equal to .50 and .65 for Hereford and Angus, respectively.

SUMMARY AND CONCLUSIONS

Data collected on 2592 calves, raised at two locations, Florida and Nebraska were used to study the importance of interactions between genotype and location on reproductive and maternal performance in beef cattle. The calves were progeny of eight different crossbred groups of dam including Angus-Hereford reciprocals, Pinzgauer-Angus, Pinzgauer-Hereford, Brahman-Angus, Brahman-Hereford, Sahiwal-Angus and Sahiwal-Hereford. Cow performance of the eight different breed groups at the two locations also were characterized.

Interactions involving breed group of dam were, in general, important sources of variation. Breed group of dam by location interaction did not influence ($P>.6$) pregnancy rate or calf survival. Birth and weaning weights and preweaning gain were significantly influenced by this interaction. The breed group of dam by location interaction for birth weight resulted in a reversal in rank at the Florida and Nebraska locations of the Brahman-Hereford and Brahman-Angus cows. Calves from Brahman-Hereford dams in Florida were heavier at birth than those from Brahman-Angus dams, but the reverse was true in Nebraska.

The eight crossbred groups of dam were classified into four groups according to breed of sire of dam. The four groups were Brahman-taurus, Sahiwal-taurus, Pinzgauer-taurus and Hereford-Angus reciprocals. Comparisons of weaning weights of progenies from the different breed groups of dam resulted in a change in the rank of Pinzgauer-taurus and Sahiwal-taurus crosses at the two locations. Calves from Pinzgauer-taurus crosses were heavier at weaning than the Sahiwal-taurus crosses when the comparison was made at the Nebraska location. The opposite was true when the two crosses were compared at the Florida location. Zebu-taurus F_1 cows weaned heavier calves at both the Florida and Nebraska locations than did the taurus-taurus F_1 cows. However, the magnitude of the difference between weaning weight of calves from these two F_1 cow groups was much greater at the Florida location.

The maternal superiority of zebu-taurus F_1 cows, along with the lack of difference in pregnancy and calf survival rates resulted in an advantage for zebu-taurus F_1 cows in terms of weight of calf weaned per cow exposed. This result leads to the conclusion that zebu-taurus crosses might be a good option for the northern states as they have been proven to be in the Gulf Coast Region. However, this conclusion should be viewed with caution, because evaluations of this nature should be conducted for a period long enough to assure the occurrence of a complete cycle of climatic variations. These variations in climate are important components of the cow response and may change the results completely.

Breed groups of dam were grouped into the same four categories as for weaning weight to evaluate preweaning gain of calf. Evaluation of these four groups indicate a change in the rank of Pinzgauer-taurus and Sahiwal-taurus dams at the two locations. Calves by Pinzgauer-taurus dams gained more weight from birth to weaning than did those from Sahiwal-taurus dams when the comparison was made at the Nebraska location. Calves by the Sahiwal-taurus dams were superior at Florida location. Calving difficulty was analyzed only for the Nebraska data. The results showed a significant interaction between breed group of dam and sex of calf. Heifer calves born to Brahman-Angus F_1 dams tended to result in a higher degree of calving difficulty than did the male progeny. The opposite trend was observed for the Sahiwal-Angus F_1 cows and no difference was observed for parturitions involving male or female calves from Brahman-Hereford or Sahiwal-Hereford F_1 cows. Among the taurus-taurus F_1 cows, however, parturitions involving male calves accounted for a majority of difficult births.

The significant interactions between breed group of dam and sex of calf found in this study for almost all traits studied were the result of a scale effect. The greater the average performance of all calves, the greater the differences between sexes. In general, it can be concluded that this interaction was, in fact, a result of the greater dimorphism exhibited by the progeny from taurus-taurus F_1 cows.

Three continuous variables, age of dam, age of calf at weaning and birth weight, were included where appropriate in the analyses of the different traits studied. Age of dam influenced pregnancy rate linearly with the percentage of pregnant cows increasing according to the equation,

$$\text{Pregnancy Rate} = .93 \pm .05 \text{ (Dam Age } -4.18).$$

The number of difficult parturitions decreased with age of dam, but the zebu-taurus F_1 cows were much less influenced by age of dam than taurus-taurus F_1 cows. This is shown by the regression equations,

$$\text{Calving Difficulty} = .98 - .13 \text{ (Dam Age } -4.18)$$

and $$\text{Calving Difficulty} = 1.25 - .38 \text{ (Dam Age } -4.18),$$

respectively, for zebu-taurus and taurus-taurus cow groups.

Weaning weight and preweaning weight gain also were influenced by the interaction between age of dam and breed group of dam. The regression equations for weaning weight were

$$\text{Weaning Weight} = 237.18 + 8.21 \text{ (Dam Age } -4.18)$$

and $$\text{Weaning Weight} = 212.56 + .15 \text{ (Dam Age } -4.18)$$

for zebu-taurus and taurus-taurus F_1 cows, respectively. A similar pattern was observed for preweaning average daily gain, with the following regression equations

$$\text{Calf Preweaning Average Daily Gain} = .97+.03\,(\text{Dam Age} -4.18)$$

and $$\text{Calf Preweaning Average Daily Gain} = .84+.09\,(\text{Dam Age} -4.18),$$

respectively, for zebu-taurus and taurus-taurus F_1 cows. Interaction between age of dam and location was significant only for birth weight. Age of dam had much more effect on birth weight of calves born in Florida than on birth weight of calves born in Nebraska. The regression equations for Florida and Nebraska were, respectively,

$$\text{Calf Birth Weight} = 28.43+1.39\,(\text{Dam Age} -4.18)$$

and $$\text{Calf Birth Weight} = 36.29+.15\,(\text{Dam Age} -4.18).$$

Age of calf at weaning influenced calf weaning weight. Calves born earlier in the season weighed more than those born later in the calving season.

As indicated by the equation,

$$\text{Calving Difficulty score} = 1.12+.009\,(\text{Birth Weight} -36.33),$$

calving difficulty increased as birth weight increased.

In conclusion, the maternal performance, measured from growth traits of the progeny, was influenced by a genotype by environment interaction. The results indicated that zebu-taurus crosses might be a good option for the northern states, but that the advantage of these crosses over taurus-taurus crosses is greater in southern regions of the U.S.

APPENDIX

TABLE A1. LEAST SQUARES ANALYSIS OF VARIANCE FOR PREGNANCY RATE

Source[a]	df	Mean squares	P
Breed group of dam (BG)	7	.015	.9390
Year (Y)	5	1.318	.0000
Location (L)	1	.146	.0704
BG x L	7	.066	.1669
Y x L	4	1.843	.0000
Age of dam: linear	1	.821	.0001
Remainder	2603	.044	

[a] The random effect of cows nested within breed group of dam was absorbed

TABLE A2. LEAST SQUARES ANALYSIS OF VARIANCE FOR CALVING DIFFICULTY, NEBRASKA LOCATION

Source[a]	df	Mean squares	P
Breed group of dam (BG)	7	2.76	.0002
Year (Y)	5	12.46	.0000
Sex (S)	1	5.95	.0030
BG x S	7	1.27	.0679
Age of dam (AD): linear	1	11.27	.0001
BG x AD linear	7	10.11	.0000
Birth weight: linear	1	13.77	.0000
Remainder	1786	.67	

[a] The random effect of cows nested within breed group of dam was absorbed

TABLE A3. LEAST SQUARES ANALYSIS OF VARIANCE FOR BIRTH WEIGHT

Source[a]	df	Mean squares	P
Breed group of dam (BG)	7	4496.40	.0000
Year (Y)	5	550.36	.0001
Sex (S)	1	9335.02	.0000
Location (L)	1	77061.30	.0000
BG x S	7	311.43	.0008
BG x L	7	343.98	.0003
Y x L	4	766.04	.0000
Age of dam (AD): linear	1	668.87	.0055
BG x AD linear	7	123.40	.1862
L x AD linear	1	435.19	.0245
Remainder	2550	85.92	

[a] The random effect of cows nested within breed group of dam was absorbed

TABLE A4. LEAST SQUARES ANALYSIS OF VARIANCE FOR WEANING WEIGHT

Source[a]	df	Mean squares	P
Breed group of dam (BG)	7	172428.25	.0000
Year (Y)	5	61808.03	.0000
Sex (S)	1	544584.35	.0000
Location (L)	1	138098.47	.0000
BG x S	7	2253.45	.2495
BG x L	7	35348.90	.0000
Y x L	4	7424.95	.0019
Age of dam (AD): linear	1	109416.27	.0000
BG x AD linear	7	12477.83	.0000
L x AD linear	1	6679.54	.0505
Age of calf: linear	1	706126.22	.0000
quadratic	1	35802.24	.0001
Remainder	2372	1742.79	

[a] The random effect of cows nested within breed group of dam was absorbed

TABLE A5. LEAST SQUARES ANALYSIS OF VARIANCE FOR SURVIVAL RATE

Source[a]	df	Mean squares	P
Breed group of dam (BG)	7	.042	.6106
Year (Y)	5	.050	.4627
Sex (S)	1	.406	.0065
Location (L)	1	.514	.0022
BG x S	7	.092	.1085
BG x L	7	.021	.9094
Y x L	4	.291	.0002
Remainder	2559	.054	

[a] The random effect of cows nested within breed group of dam was absorbed

TABLE A6. LEAST SQUARES ANALYSIS OF VARIANCE FOR AVERAGE DAILY GAIN FROM BIRTH TO WEANING

Source[a]	df	Mean squares	P
Breed group of dam (BG)	7	41283.37	.0000
Year (Y)	5	17126.35	.0000
Sex (S)	1	102702.43	.0000
Location (L)	1	15885.41	.0000
BG x S	7	624.75	.0739
BG x L	7	5331.96	.0000
Y x L	4	1421.69	.0020
Age of dam (AD): linear	1	20175.76	.0000
BG x AD linear	7	2374.89	.0000
L x AD linear	1	788.13	.1267
Remainder	2374	337.66	

[a] The random effect of cows nested within breed group of dam was absorbed

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BIOGRAPHICAL SKETCH

Kepler Euclides Filho was born November 29, 1950, in São João Del Rey, Minas Gerais, Brazil. His parents are Kepler Euclides Sant'Ana and Verônica Gomide Euclides. He is married to Valéria and has two daughters, Rayanne and Raysla, and one son, Igor.

He attended public school in Viçosa. In 1974, he received the degree Engenheiro Agrônomo from the Universidade Federal de Viçosa. In 1975, he started working at the Centro Nacional de Pesquisa em Gado de Corte of the Empresa Brasileira de Pesquisa Agropecuária. At that time, he entered the graduate school at Universidade Federal de Viçosa and, in 1977, received the Master of Science degree in animal science.

In March 1981, he entered the graduate school of the University of Florida to pursue the Doctor of Philosophy degree in animal science.

He is a member of the Sociedade Brasileira de Zootecnia, the Conselho Nacional de Engenharia e Arquitetura and the Gamma Sigma Delta Honor Society of Agriculture.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Marvin Koger

Marvin Koger, Chairman
Professor of Animal Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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